

# Role of perirhinal cortex in object perception, memory, and associations

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The perirhinal cortex plays a key role in acquiring knowledge about objects. It contributes to at least four cognitive functions, and recent findings provide new insights into how the perirhinal cortex contributes to each: first, it contributes to recognition memory in an automatic fashion; second, it probably contributes to perception as well as memory; third, it helps identify objects by associating together the different sensory features of an object; and fourth, it associates objects with other objects and with abstractions.

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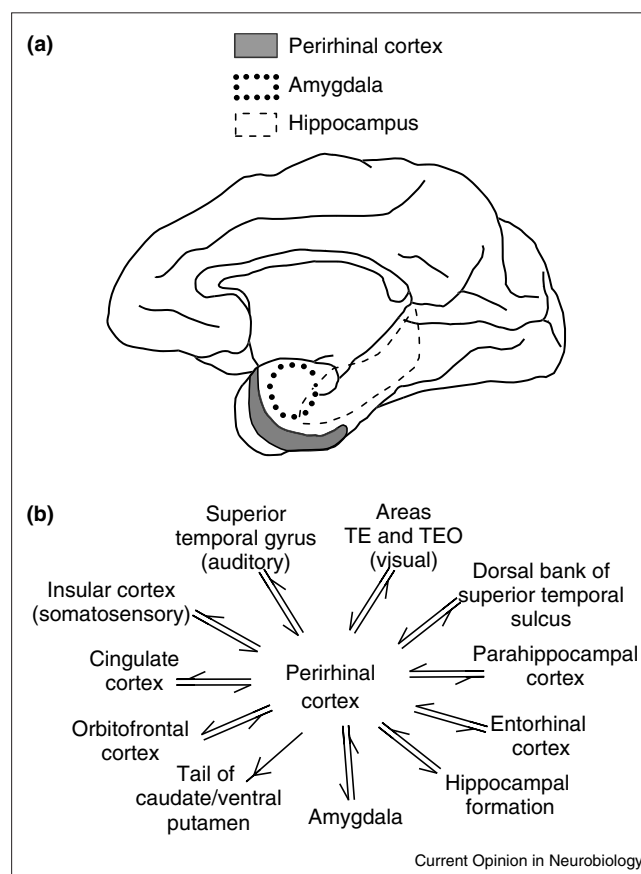
## Introduction

The perirhinal cortex lies on the ventral surface of the temporal lobe in primates and in equivalent regions in all other mammals (Figure 1a). It is a small strip of cortex, roughly 20 mm long in macaque monkeys. Although the perirhinal cortex was described as a distinct architectonic region nearly 100 years ago [1], textbooks typically neglect it entirely. Indeed, only relatively recently has the perirhinal cortex begun to be appreciated as functionally distinct from the neighboring visual cortical area TE [2,3<sup>••</sup>,4<sup>•</sup>]. Yet, perirhinal cortex plays a central role in recognizing objects. It is essential for representing an object's many attributes while recognizing that an object remains a single entity. It appears to play an important role in both the perception and memory of objects. In addition, it is important in establishing associations among objects, including abstractions such as progress toward a goal. Evidence for each of these functions is taken up, in turn.

## Object recognition

Experts widely agree that the perirhinal cortex makes an essential contribution to object-recognition memory, as measured by delayed-matching- (or nonmatching-) to-sample tasks. In these tasks, subjects must choose a currently presented object that matches (or fails to match) an object presented previously. Earlier studies showed that aspiration ablations of perirhinal cortex alone, or together with the adjacent entorhinal cortex, cause dramatic deficits in the ability of rats [5] and monkeys [6,7] to perform these tasks using vision. Recently, lesions limited to the perirhinal cortex have extended this finding to include tactile recognition [3<sup>••</sup>]. In addition, 'spontaneous' measures of

**Figure 1**



Location and main anatomical relations of the perirhinal cortex.

(a) Schematic diagram of the medial view of a macaque brain, showing the approximate location and extent of the perirhinal cortex. In this view, rostral is to the left and dorsal is up. The perirhinal cortex occupies the lateral bank of the rhinal sulcus and some of the inferior temporal gyrus just lateral to it. The amygdala and hippocampus are buried in the temporal lobe, located deep to the perirhinal cortex. (b) Major anatomical relations of the perirhinal cortex. Structures listed are regions that provide inputs or receive outputs from the perirhinal cortex. Double-headed arrows indicate reciprocal anatomical relations, whereas a single head denotes a unidirectional projection. TE and TEO are cytoarchitectonic fields in the temporal lobe [44].

recognition memory have been used. By measuring the amount of time spent exploring (in rats [8,9<sup>•</sup>]) or viewing (in monkeys [3<sup>••</sup>]) novel versus familiar objects, the role of perirhinal cortex in object recognition has been generalized to innate as well as operantly conditioned behaviors. This latter finding is underscored by physiological studies showing significantly greater activation of perirhinal cortex neurons in rats for novel versus familiar objects under passive viewing conditions [10<sup>•</sup>]. Finally, use of excitotoxic

lesions indicates that these behavioral effects probably result from cell loss in perirhinal cortex, not disruption of fibers of passage [11].

The effect of perirhinal plus entorhinal (i.e. rhinal) cortex lesions can be contrasted with that following hippocampal damage. As one would expect if perirhinal cortex plays a central role in object recognition, the greater the damage to rhinal cortex, the more profound is the object-recognition deficit; by contrast, larger lesions of the hippocampus lead to smaller deficits [12•]. These paradoxical findings suggest that a partially damaged hippocampus interferes with object recognition, rather than playing a supportive (albeit compromised) role in that function. The potential mechanisms underlying this pattern of results are elaborated elsewhere [12•]; for present purposes, we note only that the role of the hippocampus in object recognition may differ dramatically from that of the rhinal cortex.

### Object identification and discrimination

The function of perirhinal (and entorhinal) cortex appears to be central to the establishment of object representations. Objects have several coherent properties: they comprise a 'thing' even when appreciated in isolation, in different contexts, or from different perspectives. This phenomenon is sometimes known as object identification: the knowledge that a particular object is one and the same across the different instances of experience. Anatomical and behavioral studies have led to the idea that the perirhinal cortex is responsible for linking the diverse aspects of information about objects. For example, perirhinal cortex is interconnected with a broad range of sensory cortical areas representing virtually all modalities (for reviews, see [13–15]; Figure 1b). These reciprocal connections presumably provide the neural substrate for linking the representations stored in the different sensory cortical areas.

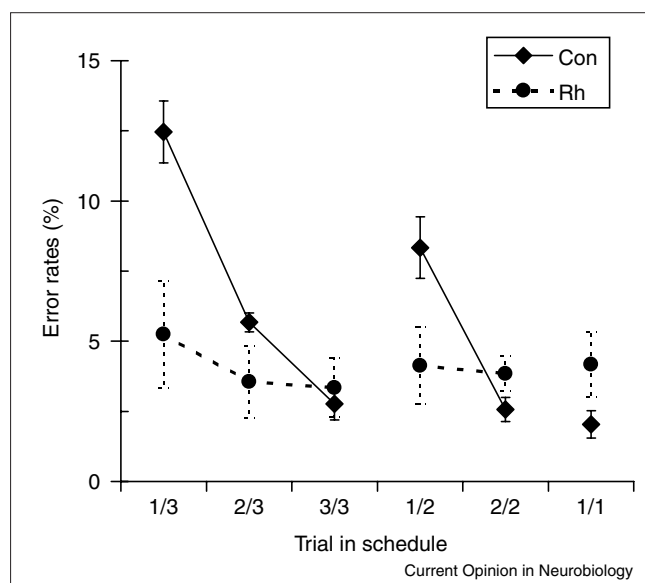
Evidence for a perirhinal cortical contribution to object identification comes from studies of discrimination learning, a task in which rats or monkeys must learn to select the same (or a different) object from a pair (or a group) of objects across trials [16–18]. Buckley and Gaffan [18] trained monkeys on a set of object discrimination problems. They presented the monkeys with pictures of objects that had been photographed from different views. When those discriminations had been learned from one set of perspectives, the monkeys were tested for their ability to learn discriminations of the same objects photographed from a different set of perspectives. If these new discriminations were learned faster than the initial set, then this would provide evidence of positive transfer. Monkeys with perirhinal cortex removals were impaired, relative to control monkeys, in transferring to the new views. Similarly, monkeys with perirhinal cortex removals are impaired on oddity tasks in which they must identify the different object among several different views of the same object [17]. In addition, unlike intact monkeys, monkeys with lesions of rhinal cortex are unable to choose a visible object first sampled by

touch [19] or first sampled by viewing part of that object [20]. It seems likely, therefore, that perirhinal cortex associates the different visual views of objects and their various nonvisual attributes (e.g. smell, texture etc.), thereby mediating object identification. Presumably, to the extent that object identity is important for a given cognitive function, the perirhinal cortex will be necessary [21–23].

Thus, at least under certain circumstances, perirhinal cortex plays an important role in both object recognition and object discrimination. However, the mechanisms underlying object recognition and object discrimination are not necessarily one and the same. After perirhinal and entorhinal cortex lesions, the magnitude of the impairments on different tests of object discrimination (e.g. concurrent discrimination of several object pairs versus discrimination of a single pair) correlated with each other, but not with the magnitude of the object recognition impairment [11]. Thus, the processes of recognition and discrimination might be subserved by at least partially separate mechanisms, both involving perirhinal cortex. In support of this idea, Hampton and Murray (unpublished data) have found that recognition deficits persist in monkeys with perirhinal cortex lesions, even when perceptual identification of the to-be-remembered stimuli is equated in operated and control monkeys. This was achieved by training monkeys on a matching-to-sample task with 56 sets of four images, and by using each set of stimuli in one trial per daily test session. The same 56 sets of stimuli were used across days, for the duration of the experiment. The monkeys were trained on matching-to-sample with 0-second delays until they could perform above 90% accuracy, and then were tested with longer, variable delays between sample and choice test. Under these conditions, using these familiar and readily distinguishable stimuli, monkeys with perirhinal cortex lesions still showed faster forgetting than controls. Although different physiological correlates of mnemonic processes have been identified in perirhinal cortex (for reviews, see [24,25]), a systematic evaluation of the neural mechanisms underlying different types of object memory has not yet been carried out.

### Object perception and memory

There is currently a controversy about whether perirhinal cortex functions in object memory but not perception [3•,26,27]. Buffalo *et al.* [3•,26,28] observed good performance on tests of object recognition memory at short delays in monkeys with perirhinal cortex removals and in humans with damage to the medial temporal lobe, including perirhinal cortex; deficits emerged only when delays between initial and subsequent (test) exposures to objects were increased. They therefore concluded that the perirhinal cortex was not important for object perception, but functioned only in object memory. However, intact performance on object discrimination or object matching tasks with short delays does not necessarily indicate intact perception of all kinds of objects under all circumstances, but only for the types of objects presented. Thus, their results

**Figure 2**

Performance on a reward schedules task after introduction of new visual cues. The graph shows the effect of perirhinal plus entorhinal (i.e. rhinal) cortex removals on monkeys' performance of a reward schedules task, in which one, two, or three color-discrimination trials had to be performed correctly to obtain reward. On each trial, a visual cue indicated progress through the sequence of trials, or schedule. That is, the 'progress cue' signaled whether the monkey was performing the first, second or third of three (1/3, 2/3, 3/3), the first or second of two (1/2, 2/2), or the only trial in the one-trial schedule (1/1). Data shown are mean performance scores (percent error) for the third and fourth weeks after new progress cues had been introduced. Whereas the controls (solid line) made the most errors on those trials furthest from reward delivery (1/3), and made progressively fewer errors as the reward approached, monkeys with rhinal cortex removals (dashed line) made few errors in any state. Thus, the operated monkeys seemed unable to associate the progress cues with their prediction about the number of trials yet to be completed. Data from [39••]. Con, unoperated control monkeys ( $N = 2$ ); Rh, monkeys with rhinal cortex lesions ( $N = 3$ ).

may not generalize to tests in which the objects are designed to tax visual perception.

Other evidence favors the idea that the perirhinal cortex contributes to both object perception and memory [17,29••]. Building on earlier suggestions that the complexity of visual representations increases as one moves rostrally within the ventral visual stream [30,31], Murray and Bussey [29••] have proposed that visual representations are organized in a hierarchical fashion, with neurons in caudal portions of the inferior temporal cortex representing simpler features, and neurons in more rostral portions of inferior temporal cortex, including perirhinal cortex, representing more complex conjunctions of features. From this viewpoint, perirhinal cortex, like other portions of the inferior temporal cortex, plays a role in the representation of visual stimuli; removal of perirhinal cortex would be predicted to disrupt an animal's ability to represent complex conjunctions of features but to leave intact the ability to represent simpler features. One implication of this idea is that the perirhinal cortex should

be especially important for the visual discrimination of objects containing a high degree of feature ambiguity — a situation that arises when a given feature (for example, the color magenta or a triangle of a particular size, shape and orientation) comprises part of both rewarded and unrewarded objects. To test this idea, monkeys with aspiration removals of the perirhinal cortex and unoperated controls were tested on a series of visual discriminations in which the number of object pairs was held constant but the degree of feature ambiguity (i.e. overlap) was varied systematically. Monkeys with perirhinal cortex lesions were unimpaired in a minimum feature-ambiguity condition, mildly impaired in an intermediate condition, and severely impaired in a maximum feature-ambiguity condition (TJ Bussey, LM Saksida, EA Murray, unpublished data; see also [32]). The impairment could not be explained on the basis of discrimination difficulty: the control subjects found the intermediate and maximum ambiguity conditions to be equally difficult. In addition, monkeys with perirhinal cortex lesions are not impaired relative to controls on difficult color discriminations [2], even ones that fall into the same range of difficulty as the discriminations in our maximum feature-ambiguity condition. Thus, the results argue for a role for perirhinal cortex in the discrimination of visual features, and therefore in object perception.

Recently, two visual tasks first used in macaque monkeys have been adapted for use in humans to assess the possibility that human perirhinal cortex is important for visual perception [33,34]. Stark and Squire [34] used the oddity task [17] described earlier. Although the objects were evidently difficult to discriminate, a comparison of the performances of amnesic patients with damage to the medial temporal lobe that either included or excluded perirhinal cortex showed that there was no added effect of perirhinal cortex damage. How can this apparent difference between the role of perirhinal cortex in monkeys and in humans be reconciled? The monkey studies have focused on feature ambiguity, whereas the clinical studies have dealt with perceptual difficulty. Perhaps perceptual difficulty *per se* is not the relevant parameter and, therefore, the perirhinal cortex in humans may be important for resolving feature ambiguity. Consistent with this idea, some data [34] suggest that accurate face discriminations, which arguably involve a high degree of feature ambiguity, require an intact perirhinal cortex.

### Object associations

The associative function of perirhinal cortex is more general than merely binding the various attributes of an object into a reified representation. It also plays a role in associating objects with other objects [20,32,35,36] and other sensory representations. For example, monkeys with rhinal cortex removals are unable to select a visible object after tasting and smelling a foodstuff that has been selectively but arbitrarily assigned to that object [37]. In general, it appears that the perirhinal cortex is necessary for linking tactile [19], gustatory [37], visual [20,32,35,36] and perhaps auditory information with objects [17,38].

The kind of information that can be associated with objects can be abstract. Liu *et al.* [4•,39••] have shown that perirhinal cortex is important for associations about sequences of trials. In these studies, monkeys were required to complete one, two or three color discrimination trials to obtain a juice reward. On each trial, a visual cue indicated progress toward the trial in which primary reinforcement could be obtained. Although the monkeys were not required to use the information provided by that 'progress' cue, they evidently associated that object with the state of progress toward the reward. The monkeys made the fastest responses and the fewest errors on trials immediately preceding reward delivery. Monkeys trained on this task were given lesions of rhinal cortex and then tested for their ability to learn the associates of new progress cues. Whereas unoperated controls used the new cues to guide their behavior as before, monkeys with rhinal cortex removals did not (Figure 2). This finding shows that rhinal cortex is essential for forming associations between objects and abstractions, such as proximity to reward, or, alternatively, ordinal position in a series [39••].

However, perirhinal cortex is not necessary for all types of object-based associations. For monkeys, some foods are generally preferred and will be retrieved given a choice between that food item and some less-preferred one. When a generally preferred food is devalued by prior feeding with that particular food, two behaviors are observed. First, monkeys instinctively change their choice and will retrieve a different kind of food. Second, monkeys that have had experience with particular object-food pairings (acquired in the context of learning a set of visual discrimination problems) will avoid responses to objects covering the devalued but generally preferred food in favor of other objects that cover a presently preferred food. Lesions that include the perirhinal cortex do not affect either of those behaviors [40]. By contrast, monkeys with amygdala removals, or with surgical disconnection of the amygdala and orbital prefrontal cortex, continue to choose objects overlying food that has been recently devalued. They can choose a presently preferred food item over one for which they are sated, as can normal monkeys, and also can use objects to obtain the food that is generally preferred [41,42]. This finding suggests a limitation in the role of perirhinal cortex in associating objects with other information. Food devaluation is a transitory state, dependent on the monkey's drive for that food at a particular time. The perirhinal cortex apparently plays little or no role in associating objects with the immediate value of some food item, although the amygdala does, in tandem with the orbital prefrontal cortex.

Evidence from anatomical, physiological and ablation studies in animals has led to the suggestion that the perirhinal cortex is an essential part of a system for storing fact-like information about objects. Most of the results on object association learning that are discussed in this article are consistent with this view. Furthermore, this 'object

knowledge' system appears to be analogous to a semantic memory system in humans. Indeed, there are parallels between the core features of semantic dementia [43] and the impairments observed in monkeys with perirhinal cortex lesions. For example, patients with semantic dementia typically have severe impairments in their ability to name a picture of an object, to link a written description of an object with a picture of that object, and to identify the typical color of objects when provided with black and white line drawings. The common theme is an inability to link the separate representations, an ability that is based on long-term associations. An evaluation of the extent of perirhinal cortex damage in patients with semantic dementia would elucidate the role of the perirhinal cortex in acquisition of knowledge about objects.

## Conclusions

The studies reviewed here show that the perirhinal cortex plays a critical role in object recognition and, in addition, a central role in object identification: the knowledge that a particular object is one and the same across the different instances in which it is experienced. In the service of object identification, perirhinal cortex associates the different views of objects and their various nonvisual attributes (e.g. smell, texture), thereby binding the various attributes of an object into a reified representation. Moreover, perirhinal cortex plays a role in associating objects with other objects and with abstractions, such as progress towards a goal. It seems likely that the perirhinal cortex plays an important role not only in memory, but also in object perception. Additional studies are needed to determine the nature of perirhinal cortical interactions with other brain structures (e.g. amygdala, hippocampus, basal ganglia) in storing different kinds of information, the precise ways in which perirhinal cortex contributes to perception, the number and types of physiological mechanisms operating within perirhinal cortex that contribute to information storage, and the extent to which perirhinal cortex contributes to object knowledge in humans.

## Acknowledgements

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disrupt tactile as well as visual recognition memory. Second, perirhinal cortex damage is shown to disrupt 'spontaneous' measures of visual recognition memory as well as rule-guided ones.

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There are two main subdivisions of the inferior temporal cortex – namely, perirhinal cortex and area TE. The present study shows that neurons in perirhinal cortex, but not in area TE, carry signals related to the different trial types in a reward schedules task. Thus, a population of such cells may carry information about progress through the sequence of trials. In addition, the results show a dissociation of function between perirhinal cortex and area TE.

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Although lesions of the perirhinal cortex have been reported to disrupt performance on some spatial tasks, the present study shows that this need not always be the case. Combined removal of perirhinal plus postrhinal cortex is found to severely disrupt performance on tests of recognition memory, but fails to disrupt performance on two different measures of spatial memory that are sensitive to hippocampal damage. Evidently, the perirhinal/postrhinal cortex is not a necessary route for spatial information to reach the hippocampus.

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A topic of central interest is the independent contributions of brain structures to different types of memory. This study measures the immediate-early gene products of *c-fos* as a sign of differential neuronal involvement in rat brains during two main conditions: first, passive viewing of novel versus familiar single objects; and second, passive viewing of novel versus familiar arrangements of arrays of objects. Perirhinal cortex and TE were differentially activated during viewing of novel relative to familiar objects, whereas the hippocampus was not. By contrast, the postrhinal cortex and CA1 were activated during viewing of novel relative to familiar arrangements of arrays of objects whereas perirhinal cortex and TE were not. Thus, the perirhinal cortex and hippocampus appear to be involved in processing information about the familiarity of single objects and of particular arrangements of arrays of objects, respectively.

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These authors present a meta-analysis of data from studies examining the effects of selective hippocampal lesions on visual recognition memory in monkeys. The results show that although selective hippocampal damage does yield a net mild impairment in recognition memory, as measured by the delayed-nonmatching-to-sample task, there is a significant inverse correlation between the extent of hippocampal damage and the magnitude of the impairment in recognition memory. Thus, paradoxically, large lesions of the hippocampus are associated with little or no recognition impairment, whereas smaller lesions are associated with moderate to severe impairment. This relationship is the opposite of that obtained for the rhinal cortex; as expected, greater rhinal cortex damage is associated with a greater magnitude of recognition impairment. These results suggest that the rhinal cortex and hippocampus make different contributions to recognition memory. Furthermore, they may be relevant to the interpretation of the effects of hippocampal damage on recognition memory in humans.

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